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Study of Adaptations of Aphids (Homoptera, Aphidinea) to Ants: Comparative Analysis of Myrmecophilous and Nonmyrmecophilous Species

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Abstract—Behavioral patterns of 4 obligatory myrmecophilous and 4 nonmyrmecophylous aphid species from the families Drepanosiphidae, Aphididae, and Lachnidae were studied in nature in the forest-park zone of the Novosibirsk Scientific Center in 1998–1999. All these species form no galls. Observations were accompanied by an individual marking of insects. The behavioral repertoires of myrmecophilous and nonmyrmecophylous species are significantly different. Defensive reactions are absent in the behavior of obligatory myrmecophilous species. Their behavior includes only elements of adaptation to trophobiosis; most of these are aimed to attract ants and communicate with them. The behavior of nonmyrmecophylous species is more flexible and diverse. It includes some elements of passive defense, from jumping off a plant to demonstration of "aggressive" poses, allowing them, at least partly, to avoid predators.

Aphids (Homoptera, Aphidinea) are small insects feeding on plant juices. The group is characterized by complicated life cycle, with cyclic parthenogenesis. With the environment conditions changing, aphids can develop into apterous or alate morphs and start to reproduce in autumn only. Alate specimens of many species migrate from one plant to another. At present, a total of about 4400 aphid species are known (Stern and Foster, 1996). In spite of their small size, aphids produce a great amount of honeydew (sweet, sugar-rich secretion), which is an important source of carbohydrates for ants. In turn, ants defend aphids from predators. Thus, the trophobiontic relationships between these two groups are mutually beneficial. In the character of aphid-ant relationship, aphids are usually divided into myrmecophilous (visited by ants) or nonmyrmecophylous species. In colonies of myrmecophilous species, ants are found virtually permanently; in nonmyrmecophylous colonies, ants may be either present or absent.

Trophobiotic relations between aphids and ants have long attracted the attention of entomologists (Mordvilko, 1901, 1936; Grinfeld, 1961; Sudd, 1987; Vepsalainen and Savolainen, 1994; Stadler and Dixon, 1999; Molnar *et al.*, 2000; Yao *et al.*, 2000). However, mainly morphological, anatomical, and physiological characters of these insects have been examined. As known, most nonmyrmecophylous aphids possess long tubules (siphons), these being reduced in myrmecophilous forms. Moreover, a preanal corolla of hairs, found in myrmecophilous species, helps to keep a honeydew drop till the appearance of an ant. In contrast to other aphids, many Lachnidae possess a filtration chamber, producing honeydew with increased sugar content (Kunkel and Kloft, 1977). The colony size and aphid fecundity have been compared in colonies with and without ants in order to assess advantages of mutual relations with ants. Nixon (1951) and Way (1963) summarized the data obtained and demonstrated that the visited colonies are larger: aphids feed more actively and produce more offspring; the probability of death is higher in colonies not visited by ants.

The attitude of ants to aphids during the first meeting depends mainly on the behavior of the latter; this phenomenon has been mentioned in the literature (Sakara, 1994). However, only separate publications have been concerned with ethological mechanisms of aphid-ant relations; in these papers, the main attention was paid to the ant behavior (Dlusskii, 1967; Hortsmann, 1973; Novgorodova and Reznikova, 1996; Reznikova and Novgorodova, 1998). Till now, myrmecophilous aphids have only been studied in relation to a narrow complex of adaptations to honeydew production; no differences in behavior between myrmecophilous and nonmyrmecophylous species have ever been examined.

Table 1. Trophic plants, number of colonies, and body size of the aphids examined

Species	Trophic plant	Number of colonies	Size group, mm		
			small	medium	large
Symydobius oblongus	*Betula verrucosa*	17	0.5–1.0	1.5–2.4	2.6–3.2
Aphis craccae	*Vicia sepium*	14	0.3–0.5	0.8–1.3	1.5–2.2
A. viburni	*Viburnum opulus*	23	0.4–0.6	0.9–1.8	2.0–2.7
Cinara boerneri	*Larix sibirica*	27	0.6–1.0	1.5–3.0	3.4–4.0
Acyrthosiphon pisum	*Pisum sativum*	13	0.8–1.2	1.5–3.5	4.0–5.5
Uroleucon cirsii	*Tragopogon orientalis*	6	0.8–1.0	1.5–3.5	4.0–4.8
Megoura viciae	*Lathyrus pratensis*	6	0.7–1.0	1.5–3.0	3.4–4.0
Hyperomyzus pallidus	*Sonchus arvensis*	10	0.5–1.0	1.2–2.4	2.5–3.0

The behavior of nonmyrmecophylous aphids has been studied mainly in gall-formers (families Hormaphididae and Pemphigidae). The data obtained demonstrate the complex nature of behavioral adaptations in these insects. As a rule, specialized castes of soldier aphids, actively defending colonies, are mainly constituted by 1st and 2nd instar larvae, and less frequently by obligatory or facultatively sterile adults (Aoki, 1977; Foster, 1990). The soldiers commonly use the stylet (proboscis) or special head processes as a weapon (Stern and Foster, 1992). Together with defending the colony, soldier aphids clean galls and also remove honeydew, exuvia, and dead aphids (Benton and Foster, 1992). Occasionally, nonmyrmecophylous aphids also use other defense methods, such as secretion of a viscous material from siphons (tubules) or secretion of the alarm pheromone (Dixon, 1958). Only two possible reactions to danger have been mentioned for aphids forming no galls: an insect can leave its feeding site (crawling to another place of jumping off the plant) or pays no attention to an irritant. The "vigilance" of aphids remained unexamined. However, exposed nonmyrmecophylous species may demonstrate rather complex behavioral stereotypes, such as, e.g., fight for a feeding site (Foster, 1996).

A comparative analysis of myrmecophilous and nonmyrmecophylous aphid species forming no galls (i.e., accessible to ants) and dwelling in the same forest was made. Individual behavioral repertoire and "vigilance" were examined. The aphid behavior was analyzed in terms of their adaptation to contacts with ants.

MATERIALS AND METHODS

The study was performed in the forest-park zone of the Novosibirsk Scientific Center in 1998–1999. Four myrmecophilous [*Symydobius oblongus* Heyd. (Drepanosiphidae), *Aphis craccae* L., *Aphis viburni* Scop. (Aphididae), and *Cinara boerneri* H.R.L. (Lachnidae)] and four nonmyrmecophylous [(*Acyrthosiphon pisum* Harr., *Uroleucon cirsii* L., *Megoura viciae* Buckt., and *Hyperomyzus pallidus* H.R.L. (Aphididae)] aphid species were studied. Representatives of these species live in colonies of several to several tens of individuals and form no galls. All aphid species of the first group are obligatory myrmecophilous forms, they were never found without ants of the genera *Formica*, *Lasius*, and *Myrmica*, at least in the area examined.

Aphids were watched in daytime (10 a.m.–5 p.m., 30 min for each individual); the total observation time constituted about 250 h). Cosmetic means were used for individual marking of aphids. Three samples of different sizes, with 20 specimens each, were considered for each species examined: small, medium, and large (Table 1). Preliminarily, insects were measured under a binocular light microscope with the use of an ocular micrometer (50 specimens of each species); in the field, the aphid body length was estimated more roughly with the use of sliding calipers or a ruler. The first group included 1st instar larvae, and the last, adults and 4th instar larvae; the medium group included 2nd and 3rd instar larvae. In all, about 500 aphids were marked.

The following experiments were performed in order to study aphid reactions to environmental stimuli:

(1) Imitation of an ant "asking for honeydew." Aphid abdomen was stroked with a preparation needle and the reaction of the aphid was recorded (100 individuals of each species).

Table 2. Reactions of nonmyrmecophylous aphid species to danger in relation to their size

Number of points	Reaction	*A. pisum*			*U. cirsii*			*M. viciae*			*H. pallidus*		
		S	M	L	S	M	L	S	M	L	S	M	L
1	Neutral	+	+	–	+	+	–	+	+	–	+	+	–
2	Dropping off a plant	+	+	–	+	+	–	+	+	+	+	+	–
3	Passing to another site	+	+	+	+	+	+	+	+	+	+	+	+
4	“Alert” pose	–	+	+	–	–	+	–	+	+	–	+	+
5	“Frightening” pose	–	–	+	–	–	+	–	–	–	–	–	–
6	Aphid “kicks”	–	–	–	–		–	–	+	+	–	+	+

Size categories: (S) small, (M) medium, and (L) large.

(2) Imitation of enemy attack. Ladybirds were put on a plant with aphids and the aphid behavior was observed during 10 min. Five adult beetles and five larvae were placed in two colonies of each species.

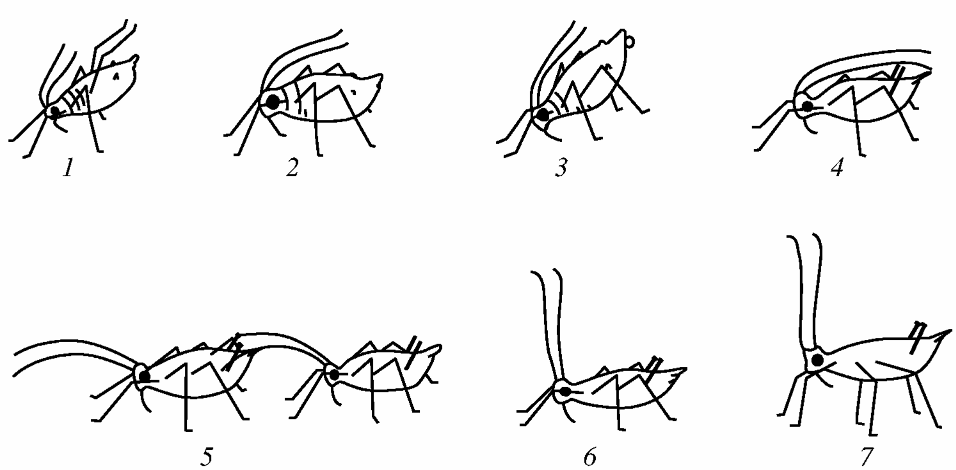
(3) In order to assess the reaction of nonmyrmecophylous species to presence of ants (*Lasius niger*) the ants were accurately placed on plants with aphids, and the aphid behavior was observed during 10 min. Five colonies of each species were examined, with 10 replications.

(4) Vigilance test. Touching of aphid antennae with a preparation needle was used as an irritant. The touching was repeated 4–5 times with 30 min intervals.

The goal of the experiments with ants placed on plants with aphid colonies was to observe the first reaction of aphids to their potential enemies till the moment of predator attack. The interval of observations (10 min) was sufficient for ladybeetles or ants to reach the aphid colony. The responses of insects to danger, arranged in order of their increasing activity, constitute a “vigilance scale,” in which the number of points corresponds to the serial number (1–6) of a behavioral element (Table 2).

RESULTS

In all, 16 behavioral elements were distinguished. Eight of these are typical of myrmecophilous, and 12, of nonmyrmecophylous species. The most characteristic poses of the aphids examined are shown in the graph. The results of our experiments (Table 3) show significant qualitative and quantitative differences in behavioral repertoire between myrmecophilous and nonmyrmecophylous species. Four common and 12 specific behavioral elements were revealed.



Poses of (*1–3*) myrmecophilous and (*4–7*) nonmyrmecophylous aphids, schematically: (*1–5*) variants of quiet position on a plant [(*3*) secretion of honeydew drop]; (*6, 7*) aggressive poses [(*6*) “alert” pose; (*7*) “frightening” pose].

Table 3. Behavioral repertoires of myrmecophilous and nonmyrmecophylous aphids

No.	Behavioral element	Myrmecophilous				Nonmyrmecophylous			
		C. boerneri	*S. oblongus*	*A. craccae*	*A. viburni*	*A. pisum*	*A. cirsii*	*M. viciae*	*H. pallidus*
	Position on a plant								
1	Hind legs raised	–	–	+	+	–	–	–	–
2	Hind legs lowered, antennae pointing forward	–	–	–	–	–	+	–	–
3	Hind legs lowered, antennae arranged along the body	+	+	–	–	+	–	+	+
	Honeydew secretion								
4	Abdomen raised	+	+	–	–	–	–	–	+
5	Hind legs make rotating movements in air	–	–	+	+	–	–	–	–
6	Drop taken-in back into abdomen	+	+	+	+	–	–	–	–
7	Drop kept at abdominal apex	+	+	+	+	–	–	–	–
8	Drop forced out of abdomen					+	+		
9	Drop thrown away with leg	–	–	–	–	–	–	+	+
	Movement on a plant								
10	Antennae along the body	+	+	+	+	+	+	–	–
11	Antennae raised	–	–	–	–	+	+	+	+
12	Antennae pointing forward	+	+	+	+	+	+	+	+
	Response to a danger								
13	Dropping down*	–	–	–	–	–	+	+	+
14	“Alert” pose**	–	–	–	–	+	+	+	+
15	“Frightening” pose***	–	–	–	–	+	+	–	–
16	Aphid “kicks”****	–	–	–	–	–	–	+	+

* Aphid jumps off a plant.
** Aphid stands motionless, stops feeding, stands with antennae raised perpendicularly to the body.
*** Aphid stands on nearly straight legs with antennae raised very high, so seeming much higher. Occasionally it also rocks up and down, bending and unbending legs.
**** Aphid sharply unbends hind legs, pushing ants away.

Behavioral Patterns of Myrmecophilous Aphids

Myrmecophilous aphids are well adapted to interaction with ants. The imitation of predator attack or vigilance test both result in a neutral reaction, when no aphid response to irritation is observed.

All myrmecophilous species produce honeydew very slowly. They can retain a drop of dew till the arrival of an ant, keeping it on the preanal tuft of hairs, or taking it in back into the abdomen. Apparently, this ability develops with age, because no adult lost honeydew drops (Table 4). Imitation of asking for honeydew results in the secretion of a drop in most of individuals (88%, 86%, 92%, and 77% in *S. oblongus*, *A. viburni*, *A. craccae*, and *C. boerneri*, respectively). In addition, some specific behavioral elements (“honeydew signals”) forego honeydew secretion, attracting ants. For example, specimens of *S. oblongus* raise abdomen apex, occasionally together with hind legs. *A. viburni* and *A. craccae* rotate their hind legs in air.

The migration propensity of aphids is mainly a species-specific character. *S. oblongus* appeared to be most mobile among all the species examined. They can go as far as 50 cm away from a colony. However, in most cases (33 out of 44, or 88.6% of all movements recorded during 3 h), aphids returned back to their colony. *C. boerneri*, *A. viburni*, and *A. craccae* virtually always remain at the same place.

Absence of ants can cause a "panic" among myrmecophilous aphids. They begin to crawl in different directions, joining, whenever possible, neighboring colonies visited by ants. We repeatedly observed how aphids left by ants passed into other colonies of the same species and stayed there if ants were "respectful," and tapped the newcomers with their antennae (37 out of 43, 12 out of 20, 18 out of 19, and 21 out of 27 cases in *S. oblongus*, *A. viburni*, *A. craccae*, and *A. boerneri*, respectively).

Behavioral Patterns of Nonmyrmecophylous Aphids

Nonmyrmecophylous ants demonstrate behavior adapted to independent existence, including some elements of passive defense. All fleas of nonmyrmecophylous species secrete honeydew very rapidly, forcing it out of the abdomen (*A. pisum* and *A. cirsii*) or throwing it away with a hind leg (*M. viciae* and *H. pallidus*). Nonmyrmecophylous aphids rapidly respond to all external irritants. The imitation of asking for honeydew is percepted either neutrally or as a negative irritant. We observed three types of responses: neutral response (92 and 100% of *A. pisum* and *U. cirsii*, respectively), going to another place (8%, 29%, and 16% of *A. pisum*, *M. viciae*, and *H. pallidus*, respectively), and "kicking" (71 and 84% of *M. viciae* and *H. pallidus*, respectively).

The responses of aphids to imitation of a host attack were different. For example, placing ladybeetle larvae in an aphid colony always resulted in a neutral reaction. Probably, this is associated with the behavior of larvae themselves: they approached the colony very slowly and always stopped at the colony border. Neither marginal, no "wandering" individuals responded to beetle larvae, apparently, because of the sluggishness of these larvae. Adult ladybeetles disturbed an aphid to a greater extent: they crawled over a plant rather rapidly, frequently touching aphids near the colony border. As a result, aphids demonstrated a variety of responses (Table 2).

Table 4. Ability of aphids of different size categories to retain honeydew till the appearance of ants

Species	Number of lost (fallen) drops, %		
	small aphids	medium aphids	large aphids
S. oblongus	13.4 ± 2.2	7.0 ± 2.4	0
A. viburni	37.1 ± 2.7	5.1 ± 1.8	0
A. craccae	26.9 ± 2.0	4.9 ± 1.7	0
C. boerneri	19.2 ± 3.36	5.8 ± 2.15	0.12 ± 0.19

Table 5. Estimation of vigilance of nonmyrmecophylous aphids, in points

Species	Size category		
	small	medium	large
A. pisum	1.4 ± 0.67	1.9 ± 1.2	4.0 ± 0.86
U. cirsii	1.6 ± 0.88	2.2 ± 1.09	4.1 ± 0.89
M. viciae	1.9 ± 0.85	2.2 ± 1.06	4.5 ± 1.64
H. pallidus	1.5 ± 0.69	2.2 ± 1.01	5.2 ± 1.23

Twenty aphids from each group were tested.

Similar responses were observed when *L. niger* ants were placed on plants with nonmyrmecophylous aphids. These ants also rapidly moved over a plant, touching aphids with antennae and legs. However, no negative after-effects for ladybeetles or ants were observed.

The behavioral patterns of nonmyrmecophylous aphids were similar within each species, not only in tests with ladybeetles and ants placed on plants with aphids, but also in vigilance tests. Six types of responses were revealed (Table 2), and aphids of different size groups demonstrated definite combinations of behavioral elements. The "vigilance scale" was used to

Table 6. Display of aggressive reactions by nonmyrmecophylous aphids of different size, %

Species	Reaction	*n*	Size category		
			small	medium	large
A. pisum	Movement toward danger	13	3.38 ± 1.39	9.39 ± 2.02	94.38 ± 3.69
U. cirsii		6	9.1 ± 2.7	9.0 ± 1.41	97.67 ± 1.63
M. viciae	Pushing potential predators away with hind legs	9	9.78 ± 2.44	37.56 ± 3.09	92.78 ± 3.77
H. pallidus		10	13.8 ± 2.35	46.6 ± 3.34	100.0 ± 0.0

n is the number of colonies examined.

show that vigilance depends on age in all cases (Table 5). Adult aphids were the most active in dangerous situations (Table 2). Usually, *M. viciae* and *M. pallidus* “kick” an enemy, whereas large aphids (*A. pisum* and *U. cirsii*) not only demonstrate a “deterrent” pose, but also frequently move in the direction of danger. At the same time, small and medium larvae of these species tried to avoid a collision (Table 6).

DISCUSSION

The behavioral patterns of myrmecophilous and nonmyrmecophylous species differ significantly, not only in the number of behavioral reactions, but also in their composition. This result is rather striking, because a comparison of ethograms of different ant species and even genera (Reznikova and Bogatyreva, 1984) showed that all differences, although occasionally significant, are mainly quantitative. In ants, species-specific behavioral acts are very few in number.

First, specific processes are associated with honeydew secretion. Myrmecophilous aphids can secrete a drop of secret virtually at any instant of time, but do it mainly when trophobiontic ants appear, in response to their specific behavior of asking for honeydew. This phenomenon not only makes myrmecophilous aphids more attractive for ants, but, apparently, decreases the probability of ant attack. As known, ants not only nurse aphids, but also hunt for them (Way, 1963; Skinner and Whittaker, 1981), occasionally using the same species for both purposes (Cherix, 1987). When an ant has to decide whether to attack an aphid or not, this decision depends on aphid behavior. For example, *L. niger* ants less frequently attack aphids offering honeydew (Sakata, 1994).

It is necessary to note that the ant “milking” behavior and trophallaxis (exchange of liquid food with other specimens of the same species) are similar in pattern. Kloft (1959) noted a certain similarity between the caudal part of an aphid and ant head and assumed that this phenomenon provokes ants to begin their “asking-for-food” behavior. Apparently, offering of food to ants by aphids can be treated as an act of “pacification” of ants, as it occurs in situations when ants use the trophallaxis for demonstration of submission (Zakharov, 1972; Reznikova, 1983). Moreover, there exists a definite system of communication between ants and aphids. Ants asking for food stroke the aphid abdomen with specific movements. As a rule, honeydew secretion occurs after several seconds of contact (Douglas and Sudd, 1980). In its turn, myrmecophilous aphids also perform some specific movements preceding the appearance of a honeydew drop. Most likely, “honey signals” serve as means of communication between aphids and ants, provoking ants to collect honeydew. A similar behavior was also observed in other myrmecophilous insects. In copper caterpillars, close association occurs between the activity of the nectar organ and palps making “honey signals.” These signals inform the convoying ants that caterpillars can supply them with food as a “reward “ (Burghardt and Fieder, 1996). Apparently, such a system of communication between myrmecophilous insects and ants makes the interaction between them more efficient.

In contrast to myrmecophilous aphids, nonmyrmecophylous species do not try to keep the honeydew. As known, accumulation of secretions produced by these insects on plant leaves and twigs leads to development of soot dew. These fungi are harmful both for plants and for aphids. Nonmyrmecophylous aphids solve this problem, throwing honeydew drops by different methods to far distances. As a result, a new danger appears: predators can find aphid colonies marked by honeydew at base of a plant. The honeydew problem is less important for myrmecophilous aphids, because ants collect most of the dew; either directly from aphid colonies or from leaves and twigs. In addition, ants defend aphids from predators rather effectively.

Nonmyrmecophylous aphids develop their own defensive mechanisms. We found that these aphids rapidly react to danger, responding to any irritation by demonstrating some elements of passive defense, aimed to avoid negative after-effects. At the same time, imitation of “asking for the honeydew” did not result in any specific response and consequent secretion of the honey in nonmyrmecophylous aphids. The response to such an irritation was the same as the response to one of our experimental irritations. In some cases, sterile 1st instar larvae fulfilled soldier functions, actively defending aphid colonies (Foster, 1990; Stern and Foster, 1996). However, adults and large last-instar larvae were most vigilant in all the species examined.

Stern and Foster (1996) mentioned in their review that Inbar (unpublished data) was the first to reveal unusual soldier aphids of the tribe Fordini (Pemphigidae). He also examined the defensive behavior in adult aphids developing from similar aggressive 1st instar larvae. However, we failed to find any aggressive reactions in aphids of junior stages. Moreover, in comparison with soldier aphids, the defensive behavior of adults of 4 nonmyrmecophylous species examined cannot be named really aggressive, because no negative effects of this behavior for potential predators (ladybeetles), or ants placed on plants with aphid colonies, were found. In contrast to the caste of soldier aphids, adults never used their stylets as a weapon, trying only to frighten "occupants" or to drive them away, taking aggressive poses or pushing enemies away. Nevertheless, such a defensive behavior is, apparently, rather effective, allowing aphids to win time necessary for crawling away or jumping off a plant.

It is necessary to note that, in our experiments, nonmyrmecophylous aphids did not respond to ladybeetle larvae. Apparently, the main reason for differentiated aphid behavior toward predators is inherent in the mechanism of enemy recognition. Behavioral patterns and chemical signals play an important role in this mechanism. Pheromones secreted by aphids via tubules, and also the odor of the haemolymph from damaged attacked aphids, can serve as alarm signals (Stern and Foster, 1996).

The problem of enemy recognition needs additional special examination. We can only assume that, in our experiments, the neutral response of aphids to ladybeetle larvae can be associated with the sluggishness of larvae. In comparison to adult beetles, they never make fast movements and jogs, moving slowly. In addition, larvae did not contact with aphids, stopping at the border of a colony and not touching aphids. Probably, in the species examined, the secretion of the alarm pheromone occurs only after direct contact with a potential predator.

Thus, the behavior of obligatory myrmecophilous species includes only elements adapted to trophobiosis. The majority of these adaptations is aimed to attract attention of ants and to communicate with them, and also to make longer the period of time when sweet secretions stay at the apex of abdomen or inside it, prepared to be given to ants. No defensive reactions are present in their behavior. Moreover, aphids commonly respond to most of irritations by secreting a honeydew drop, offering a kind of a "bribe" and demonstrating "humility and obedience."

The behavior of the nonmyrmecophylous aphids is more complicated, varying from passive defense (jumping off a plant) to demonstration of "aggressive" poses. Aphids recognize ants as usual irritators, responding to them as to enemies. Some adaptations are aimed to remove the honeydew and prevent its accumulation on plant leaves. On the whole, the behavior of nonmyrmecophylous aphids is more flexible and diverse, allowing them to avoid predator attacks, at least partly.

We examined the behavioral models of aphids with extreme degrees of myrmecophily (obligatory myrmecophilous and nonmyrmecophylous aphid species). The results obtained can serve as a basis for determining the place occupied in this scheme by facultatively myrmecophilous aphid species. These will be the main objects of future investigations.

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REFERENCES

1. Aoki, S., *Colophina clematis* (Homoptera, Pemphigidae), an Aphid Species with "Soldiers", *Kontyû*, 1977, vol. 45, n pp. 276–282.
2. Benton, T.G. and Foster, W.A., Altruistic Housekeeping in a Social Aphid, *Proc. Roy. Soc. Lond., Ser. B.*, 1992, vol. 247, pp. 199–202.
3. Burghardt, F. and Fielder, K., Myrmecophilous Behaviors in Caterpillars of the Butterfly, *Polymatus icarus* (Rottenburg, 1975): Temporal Patterns and Dependency (Lepidoptera: Lycaenidae), *Nota Lepidopt.*, 1996, vol. 19, nos. 3–4, pp. 212–229.
4. Cherix, D., Relation Between Diet and Polyethism in *Formica* Colonies, *Behav. Soc. Ins.*, 1987, vol. 54, pp. 93–115.
5. Dixon, A.F.C., Escape Responses Shown by Certain Aphids to the Presence of the Coccinellid, *Adalia decepmunctata* (L.), *Trans. Royal Entomol. Soc. London,* 1958, vol. 10, pp. 319–334.
6. Dlusskii, G.M., *Murav'i roda Formica* (Ants of the Genus *Formica*), Moscow: Nauka, 1967.
7. Douglas, J.M. and Sudd, J.H., Behavioral Coordination Between an Ant and the Aphid it Tends, *Animal Behav.*, 1980, vol. 28, pp. 1127–1139.
8. Foster, W.A., Experimental Evidence for Effective and Altruistic Colony Defense Against Natural Predators by Soldiers of the Gall-Forming Aphid *Pemphigus spyrothecae* (Hemiptera: Pemphigidae), *Behav. Ecol. Sociobiol.*, 1990, vol. 27, pp. 421–430.
9. Foster, W.A., Dueling Aphids: Intraspecific Fighting in *Astegopteryx minuta* (Homoptera: Hormaphididae), *Animal Behav.*, 1996, vol. 51, pp. 645–655.

10. Grinfeld, E.K., The Origin of Symbiosis Between Ants and Aphids, *Vestnik Leningrad. Go. Univ.*, 1961, vol. 5, pp. 73–84.
11. Hortsmann, K., Untersuchungen zur Arbeitstellung unter den usserdienstarbeiterinnen der Waldameise *Formica polyctena* Foester, *Z. Tierpsychol.*, 1973, vol. 32, pp. 532–543.
12. Kloft, W., Versuche einer Analyse der trophobiotischen Beziehungen zwischen Ameisen und Aphiden, *Biol. Zentralblatt.*, 1959, vol. 78, pp. 863–870.
13. Kunkel, H. and Kloft, W., Forschritte auf dem Gebiet der Honigtau-Forschung, *Apidologie*, 1977, vol. 8, pp. 369–391.
14. Molnar, N., Kovacs, E., and Galle, L., Habitat Selection of Ant-Tended Aphids on Willow Trees, *Tisia*, 2000, vol. 32, pp. 31–34.
15. Mordvilko, A.K., A Contribution to the Biology and Morphology of Aphids, *Trudy Russ. Ent. O–va*, 1901, vol. 33, pp. 418–485.
16. Mordvilko, A.K., Ants and Aphids, *Priroda*, 1936, vol. 4, pp. 44–55.
17. Nixon, G.E.J., *The Association of Ants With Aphids and Coccids*, London, 1951.
18. Novgorodova, T.A. and Reznikova, Zh.I., Ecological Aspect of Ant-Aphid Interactions in the Forest-Park Zone of the Novosibirsk Scientific Center, *Sib. Ecol. Zh.*, 1996, nos. 3–4, pp. 239–245.
19. Reznikova, Zh.I., *Mezhvidovye otnosheniya murav'ev* (Interspecific Relations in Ants), Novosibirsk: Nauka, 1983.
20. Reznikova, Zh.I. and Bogatyreva, O.A., Individual Behavior of Ants of Different Species at Feeding Site, *Zool. Zh.*, 1984, vol. 63, no. 10, pp. 1494–1503.
21. Reznikova, Zh.I. and Novgorodova, T.A., Distribution of Roles and Information Exchange in Groups of Worker Ants, *Uspekhi Sovr. Biol.*, 1998, vol. 118, no. 3, pp. 345–357.
22. Skinner, G.J. and Whittaker, J.B., An Experimental Investigation of the Interrelationships Between the Wood Ant (*Formica rufa*) and Some Tree-Canopy Herbivores, *J. Anim. Ecol.*, 1981, vol. 50, pp. 313–326.
23. Sakata, H., How an Ant Decides to Prey or to Attend Aphids, *Rev. Pop. Ecol.*, 1994, vol. 36, no. 1, pp. 45–51.
24. Stadler, B. and Dixon, A.F.G., Ant Attendance in Aphids: Why Different Degrees of Myrmecophily?, *Ecol. Ent.*, 1999, vol. 24, pp. 363–369.
25. Stern, D.L. and Foster, W.A., The Evolution of Soldiers in Aphids, *Biol. Rev.*, 1996, vol. 71, pp. 27–79.
26. Sudd, J.H., *Ant Aphid Mutualism, Aphids: Biology, Natural Enemies, and Control*, Amsterdam, 1987, pp. 355–365.
27. Vepsalainen, K. and Savolainen, R., Ant-Aphid Interaction and Territorial Dynamics of Wood Ants, *Memor. Zool.*, 1994, vol. 48, pp. 251–259.
28. Way, M.J., Mutualism between Ants and Honeydew Producing Homoptera, *Ann. Rev. Ent.*, 1963, vol. 8, pp. 307–344.
29. Yao, I. Shibao, H., and Akimoto, S., Costs and Benefits of Ant Attendance to the Drepanopsid Aphid *Tuberculatus quercicola*, *Oikos*, 2000, vol. 89, pp. 3–10.
30. Zakharov, A.A., *Vnutrividovye otnosheniya u murav'ev* (Intraspecific Relations in Ants), Moscow: Nauka, 1972.